

PALEOECOLOGY AND BIOSTRATINOMY OF THE UPPER

TRIASSIC TUBE FOSSILS *TITAHIA CORRUGATA* AND*TEREBELLINA MACKAYI*

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ABSTRACT

Titahia corrugata Webby, and *Terebellina mackayi* Bather, are agglutinated tube fossils that are found in the Upper Triassic (?Kaihikuan-Warepan) rocks of New Zealand. These fossils are found widely in the Torlesse Supergroup but also occur in the Tuapeka Group, South Otago. *Terebellina mackayi* has also been found in an Oretian sequence of the Murihiku Supergroup (Begg, Cave and Campbell, in press). Although commonly found lying on bedding planes or randomly oriented within beds, both taxa lived with the tube oriented perpendicular to the sediment-water interface. The organisms that constructed the *Titahia* and *Terebellina* tubes remain enigmatic but were probably suspension feeders rather than browsers, deposit feeders or active predators. Paleo-ecological segregation of the two genera may be related to differing environmental requirements. *Terebellina* probably lived in a fine grained black siltstone substrate rich in organic detritus, *Titahia* probably inhabited similar fine grained substrates but was also capable of occupying sandy sea-bottoms.

KEYWORDS: Upper Triassic, paleoecology, agglutinated tube fossils, *Titahia*, *Terebellina*, suspension feeders.

INTRODUCTION

Terebellina (=Torlessia) *mackayi* Bather, and *Titahia corrugata* Webby, are agglutinated tube fossils of uncertain taxonomic affinities. The synonymy of *Torlessia* Bather (1905) and *Terebellina* Ulrich (1904) has been established (Cave, 1982) and will be documented elsewhere. Both taxa occur widely, but generally not abundantly within ?Kaihikuan-Warepan (Ladinian-Norian) rocks of the Torlesse

Supergroup (Campbell and Warren 1965, Force and Force 1978) and both also occur in the Tuapeka Group (Campbell and Campbell 1970). *Titahia corrugata* and *Terebellina mackayi* have an overlapping time range; *Terebellina* possibly ranging from the Kaihikuan to Lower Warepan (Force and Force 1978) while *Titahia* occurs in Otamitan to Oretian rocks.

Terebellina is now also known from the Murihiku Supergroup, Wairaki Hills, Southland (Begg, Cave and Campbell, in press). More than 200 collections of these fossils are now recorded from Torlesse rocks of the South Island, but until now, studies of the mode of life and possible behaviour of these organisms have been neglected. Collections made in the Mathias River, at Arthur's Pass and in the Ashley Gorge, give a clear indication of at least some aspects of the ecology of these taxa.

THE MORPHOLOGY OF *TITAHIA* AND *TEREBELLINA*

The dimensions and morphology of these fossils have been described and figured many times (e.g. Bather 1905, Morgan 1908, Webby 1958, 1967, Campbell and Campbell 1970) and only the important features need to be summarised here. Both *Titahia corrugata* and *Terebellina mackayi* are agglutinated tubes with walls composed of detrital quartz or occasionally feldspar grains held together by a siliceous cement. The tube material is well sorted and fine grained with grain size averaging between 0.02 mm and 0.06 mm (medium to coarse silt). Slightly coarser grains (up to 0.1 mm, i.e. very fine sand) have occasionally been incorporated into the tube walls of larger specimens of *Titahia*.

Specimens are small to medium sized (1-2 mm wide and several mm long up to 10 mm wide and 70 mm long) with *Titahia* being typically larger than *Terebellina* (see Andrews, Speden and Bradshaw 1976). *Terebellina* is a simple, smooth to faintly striated longitudinally, or less commonly transversely, cylindrical or slightly tapering tube. The tube wall is up to 1 mm thick. The external diameter is variable, ranging from 1 mm up to 10 mm thick for compressed individuals. The longest tube recorded exceeds 40 mm but tubes between 20 mm and 30 mm are more common. *Titahia* is a sculptured tube, bearing numerous longitudinal ribs or corrugations that may branch. These ribs project outwards for up to 2 mm, and are typically 1 mm wide and separated by interspaces 1-1.5 mm wide. The tube wall is thick, commonly as much as 2 mm and the tube is long, with incomplete specimens reaching over 70 mm in length. Almost all specimens held in New Zealand collections are incomplete.

Although both *Titahia* and *Terebellina* are commonly described as being slightly tapering, it is generally not clear whether the tubes are open ended cylinders or cones closed at one end. However, very small *Terebellina* tubes that I have seen at Titahi Bay, Wellington (Auckland University Repository No., AU8899) and at the Lower Waimakariri Gorge bridge (c.S75/f501) appear to close at one end as does the specimen of *Titahia corrugata* from Jacks Hill, Mathias River that is indicated in Fig.1.

Several specimens of *Terebellina mackayi* display abrupt changes in tube diameter (Fig.2), but because this was seen in only a few specimens its functional significance is uncertain. It may represent a normal ontogenetic growth step, or an aberrant growth form caused, for example, by injury and only occurring in a few members of the species. More typical *Terebellina* specimens are slightly tapering with a gradual, even increase in diameter of the tube.

MODE OF OCCURRENCE

Specimens of *Titahia* and *Terebellina* are found mostly aligned or randomly oriented on bedding planes or oblique to bedding, particularly in some fine grained units. Tubes are occasionally found oriented perpendicular to bedding. Specimens lying on the bedding plane are invariably flattened, and often abraded and fragmentary (Andrews 1974, Hicks 1981). These are interpreted as representing transported faunas removed from their life position by erosion and scattered by bottom currents. Fragmentary material lying at various oblique angles within beds (e.g. Campbell and Campbell 1970, Campbell and Pringle 1981) are interpreted as essentially *in situ* assemblages that have been disrupted by bioturbation (Speden 1976), and possibly predation and compaction effects. Occurrences of *Terebellina mackayi* in black siltstones at Arthur's Pass belong to this category, and are associated with the trace fossil *Helminthopsis* and often intense bioturbation.

The habitat of *Titahia* and *Terebellina* is poorly described in the literature, although Bather (1905, p.537) stated that "*Torlessia*" lived "vertical in marine mud". Campbell and Campbell (1970) noted that some specimens of *Titahia* from the Tuapeka Group occurred more or less perpendicular to bedding and considered that these tubes were probably in life position. Webby (1967) on the other hand, believed that these organisms lived on the muddy sea-bottom rather than in it. Andrews (1974) suggested that the tubes he collected at Broken River lived oriented oblique to the sediment-water interface. My examination of his collections indicates that the Broken River material has suffered post-mortem disruption by bioturbation. Evidence presented below (especially Fig. 1) indicates that both *Titahia corrugata* and *Terebellina mackayi* lived oriented perpendicular to the sea-bottom, typically in fine grained substrates.

MODE OF LIFE

Members of an Alpine Processes party (National Water and Soil Conservation Organisation) undertaking a geological study of the Rolleston Range (Rakaia watershed) found, in 1980, the specimen of *Titahia corrugata* which prompted the writing of this paper. The specimen was found loose on Jacks Hill, east of Mistake Creek, a tributary of the Mathias River (NZMS 260, J34/f33; the specimen

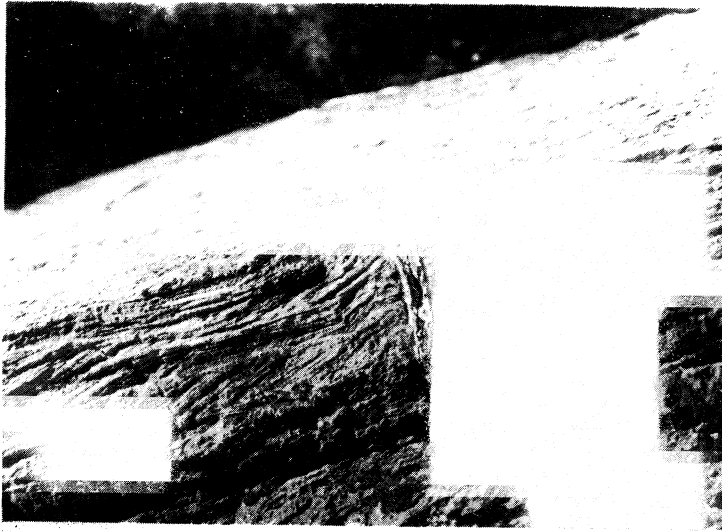


Fig. 1.

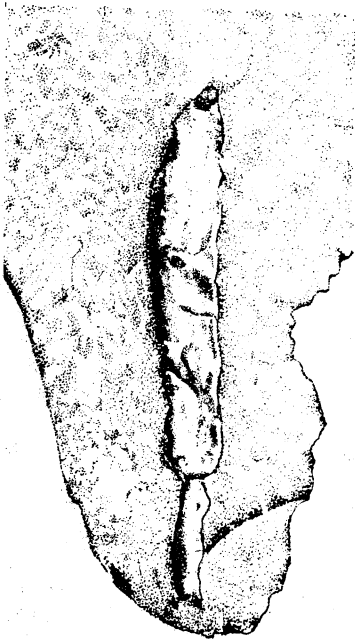


Fig. 2.

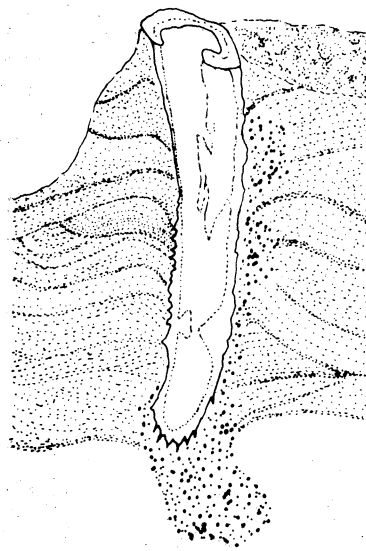


Fig. 3.

has no collection number, but is on permanent display in the Alpine Museum, Arthur's Pass National Park.

This specimen clearly shows that the organism was infaunal, living vertical in the sediment and that the tube apparently opened into seawater at or immediately above the sediment-water interface. The presence of flattened tubes lying on the bedding plane suggests that this was a precarious existence.

While the soft parts of the organism that constructed the *Titahia* tube have not been preserved, the mode of occurrence of this individual does allow some inferences as to feeding behaviour at least. Because the tube opened into water and not sediment, it is evident that the organism was most likely a suspension feeder and not a browser, deposit feeder or active predator. *Titahia* was possibly a passive predator. Further inferences as to the feeding behaviour and habitat of *Titahia* are unwarranted in light of present evidence.

It is not clear how the organism buried itself in the sediment. Close examination of the specimen in Fig. 1 clearly indicates the presence of deformed cross-beds and homogenised sediment immediately adjacent to the tube fossil (Fig. 3). These structures could have been produced during the emplacement of the tube or, alternatively, are the result of dewatering during sediment compaction and therefore has no bearing on the mode of life of *Titahia*. The absence of downwarped cross-beds anywhere except adjacent to the tube fossil suggests that the structures were more likely to be the result of the emplacement of the *Titahia* tube and not related to the overall compaction of the sediment. Similarly, the homogenised sediment occurs on the right hand side of the tube and bulges to about 1 cm below the fossil but is absent elsewhere within the same bed. The structures are therefore probably not the result of compaction.

Well preserved specimens of *Terebellina mackayi* oriented perpendicular to bedding occur in some area, for example, the Ashley Gorge (see localities tabulated in Campbell and Warren 1965). These are also interpreted as life assemblages. Fragmentary, flattened tubes that are randomly oriented with respect to bedding also occur at the Ashley Gorge localities. Examination of some outcrops show that "islands" of well preserved life assemblages

Fig. 1. Photograph of specimen of *Titahia corrugata* (J34/f33, Jack's Hill, Mathias River); specimen 2/3 natural size. Although it is perhaps not clear on this photograph, the strata face towards the top of the page.

Fig. 2. Sketch of a specimen of *Terebellina mackayi* (s75/f501 (NZMS 1 coll. No.) O.U. coll. JDC No. 1326; Lower Waimakariri Gorge bridge); specimen shows marked growth jump. Approximately 2x natural size.

Fig. 3. Sketch of the specimen of *Titahia corrugata* photographed in Fig.1 showing the down-warping of cross-beds and homogenisation of sediment immediately adjacent to the tube fossil. Approximately natural size.

are surrounded by an expanse of bioturbated sediment containing fragmentary material.

Both *Titahia* and *Terebellina* had a similar mode of life but the marked morphological differences between the two fossils suggests that they differed in at least some of their ecological requirements. Both Campbell and Campbell (1970) and Andrews (1974) note a geographic but not stratigraphic segregation of *Titahia* and *Terebellina*. Campbell and Campbell (1970) also note that *Titahia* occurs in association with coarser grained lithologies than *Terebellina*. This, and the cross-bedding indicated in Figure 1, suggests that *Titahia* may have preferred a relatively vigorous, current-swept, silty to sandy sea-bottom. *Terebellina* on the other hand, appears to have preferentially occupied parts of the sea floor lacking current action where finer grained, organically rich black silts accumulated. It is thus likely that the formation of thicker tube walls and pronounced ribs, and the tendency to greater size in *Titahia* was of assistance in maintaining stability in a current agitated sea floor environment. Because *Terebellina* preferred or required a lower energy environment, morphological specialisation was probably unnecessary and a simple, less robust tube utilised. The occurrence of life assemblages of *Titahia corrugata* in organically rich black siltstones as well as in coarser lithologies suggests that, in general, this species had a broad habitat overlapping with that of *Terebellina*.

SUMMARY

Titahia corrugata and *Terebellina mackayi* are two rather enigmatic tube fossils having agglutinate tube walls composed of mainly quartz grains held together by a siliceous cement. Although both fossils commonly occur either as current reworked bedding plane assemblages or as obliquely oriented assemblages within beds, they probably lived vertically in the sediment and were suspension feeders. The robust construction, larger size and strong longitudinal ribs of *Titahia* probably represents a response to higher energy sea floor conditions. In the quieter conditions that *Terebellina* preferred, these characteristics did not develop.

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